Display response of the Jacky Dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: A semi-Markovian process

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Abstract   Movement-based visual signals are widely distributed among animal species. They are used in a variety of contexts including mate-choice, pursuit deterrence, alarm signalling and opponent assessment. Important contributions to general theories of animal communication have been made using lizards as model systems. However, much of this work has focused on the iguanids of North and South America. The agamid lizards of Australia have received little attention even though many species are characterized by complex visual displays. Here we present a detailed description of the push-up display of the Jacky Dragon (*Amphibolurus muricatus*), which comprises five distinct components, including tail-flicks, foreleg waves, and push-ups. Rival males exchange displays when competing for territory, but little is known about the rules that govern their expression. We set up simulated intrusions in a captive setting to overcome the inherent difficulty in observing these interactions in the field. An 'intruder' housed in a small tank was positioned in front of a larger enclosure containing a 'resident' male. The response of the resident was video-taped for subsequent analysis. We first examined characteristics of the initial display bout and explored sources of variation within and between residents. Measurements included bout duration, the number and hold duration of push-ups, the total number of components, and limb preferences during foreleg waves. Markov analysis was then used to measure serial dependencies among display components. This showed that the push-up display is a semi-Markovian process: the preceding component predicted the next one with high accuracy. The display is highly constrained irrespective of whether the bout was the first or subsequent response to an intruder, and irrespective of substrate, intruder identity and resident identity. These data are an important first step in understanding the design, perception and function of movement-based visual signals in agamid lizards.

Key words: agamid lizard, Markov analysis, movement-based display, signal design, visual communication.

INTRODUCTION

The diversity of animal signals can be attributed to evolutionary forces acting in response to sexual selection (Andersson 1994), the environment (Endler 1992), receiver sensory systems (Rowe 1999), predation risk (Stoddard 1999) and social organization (Blumstein & Armitage 1997). Signals are used in a variety of contexts, including mate-choice (Hebets & Uetz 1999), parent–offspring interactions (Main & Bull 1996), foraging (Evans & Evans 1999), predator deterrence (Hasson 1991), and territory defence (Carpenter 1978). Movement-based visual signals have long fascinated biologists (Darwin 1871), and lizards have proved to be very useful model systems for studying their design and function (Fleishman 1988; Martins 1994b; Leal & Rodriguez-Robles 1997). A

useful context in which to study movement-based signals is that of animal conflicts, which do not always escalate into fights (Maynard Smith & Price 1973). Exchanges of territorial displays often allow rivals to ascertain relative status from a distance (Zahavi 1977), so that physical combat can be avoided.

Detailed descriptions of signal structure underpin research into animal signals and provide the foundation for explorations of signal function and perception, as well as other aspects of social behaviour and ecology. The diversity we see in display structure directly reflects ecological factors including habitat choice, resource distribution, presence of sympatric congeners and predation threat. Effective signals are those that have a high 'signal-to-noise' ratio. The physical habitat acts as background noise that sets a minimum structure for reliable detection in terms of the spectral characteristics (Fleishman *et al.* 1997), and relative movement of, the signal and wind-blown plants (Peters & Evans 2003). The environment will also influence the degree to which the signal degrades over viewing distance (Endler 1992). As a consequence, relatively simple

displays are favoured when longer transmission distances are required (Jenssen 1978). However, the need to remain inconspicuous to predators imposes an important constraint on display structure. Simple displays are also more common when resource defence is rare, as is likely to be true for many herbivorous lizard populations (Ord & Blumstein 2002). Conversely, when resources are limiting, we typically see more complex signals, driven by higher levels of male–male competition (Ord et al. 2001).

Stereotypy is a common property of many types of signals because it serves to increase the reliability of detection (Wiley 1983). The displays of iguanid lizard species are highly stereotyped (Carpenter & Ferguson 1977; Jenssen 1977). Lizards use either a single species-specific display (Jenssen 1975), or one chosen from a limited repertoire (Stamps & Barlow 1973; Crews 1975; Rothblum & Jenssen 1978). However, most feature a core, predictable sequence of motor patterns (Jenssen 1977). These can be highly consistent within a species, or show significant individual differences. Low variation in display patterns probably evolved for species recognition (Rothblum & Jenssen 1978). Selection pressure is therefore likely to be greater in the presence of sympatric congeners. Furthermore, when the influence of female mate choice is negligible (as appears to be the case in iguanian lizards; Tokarz 1995), the level of display divergence may reflect the extent of differential resource use, with more similar displays being retained when resource requirements overlap and are competed for between species. In contrast, displays that show considerable interspecies variation imply a species recognition role.

Most of our knowledge of movement-based lizard visual displays is based upon the iguanids of North and South America (see Ord & Blumstein 2002 for a list of species and associated references). The agamid lizards, prominent in Australia, have received comparatively little attention, despite the prevalence of motor patterns in their social behaviour (although see Mayhew 1963; Carpenter et al. 1970; Mitchell 1973; Cogger 1978; Gibbons 1979; Greer 1989). Amphibolurus muricatus is an Australian agamid lizard, native to south-eastern Australia, which inhabits dry schlerophyll forests, rocky ridges and coastal heathlands (Cogger 1996). It relies on visual motion cues to detect suitable prey items (insects and other small arthropods) and aerial predators, as well as to communicate with conspecifics. The visual display repertoire of this species was originally described following observations of a single captive male (Carpenter et al. 1970). The central feature is a 'jerky' push-up whereby the snout is pointed upward accompanied by extension of the front legs, followed by a rapid lowering of the head. The lizard either repeats these motor patterns, or moves rapidly to a new site. Other movements that may accompany the display include 'twitching or swishing' of the tail, interpreted as

a release of excitement energy, and 'rapid circumduction' of one foreleg. Recent fine-scale analysis of the display motor patterns has shown that the circumduction described by Carpenter is better described as separate forward and backward foreleg waves ('arm-waves'), while the rapid lowering of the body involves movement that travels anterior to posterior as the 'body rocks' (Peters et al. 2002). The display therefore comprises five distinct motor patterns (henceforth called 'components'): tail-flicks, backward arm-waves, forward arm-waves, push-ups and body-rocks.

In the present paper we build upon the original descriptions of the visual display by A. muricatus by Carpenter et al. (1970). We begin by exploring variation in the response of resident males to conspecific male intruders in terms of response latency and characteristics of the first display bout. Measurements include the duration of tail-flicks and the display bout, the number and hold duration of push-ups, as well as the total number of components in the bout. Recent work in anuran amphibians suggests lateralization of foreleg use in some contexts (Bisazza et al. 1996), so we also examine the choice of arm used in the backward and forward arm-waves. Finally, we determine the relative frequency of display components and analyse serial dependencies (transition probabilities) among components. These data are a first step in a research program that has broad aims of understanding the visual ecology of a native Australian lizard, as well as building on current knowledge regarding the design of movement-based animal signals and the evolution of communication systems generally.

METHODS

Subjects

Fourteen male A. muricatus were captured in the Botany Bay National Park, south of Sydney, Australia, in February and March 1999. The lizards ranged in size from 22.5 g, 89 mm SVL (snout–vent length) to 44.5 g, 107 mm SVL, and were all sexually mature (as per Harlow & Taylor 2000). Each animal was wormed on arrival and held in a glass aquarium (36 cm × 92 cm and 38 cm high), with cardboard screens to ensure animals could not see their neighbours. After approximately 4 weeks, lizards were transferred into larger pens (64 cm × 150 cm and 120 cm high) constructed from aluminium frames, with rigid plastic sheeting for the sides (opaque white), and a transparent perspex front. Pens were arranged along one wall to maintain visual isolation. All aquaria and pens contained sand substrates, with branches suitable for basking and vegetation providing refuge. Lizards were maintained on a 14 h : 10 h light : dark cycle, corres-

ponding to mid-summer. Heat lamps (125 W, 240 V Philips Spotone) and UV lamps (300 W Osram Ultra-Vitalux) were suspended above the aquaria, allowing behavioural thermoregulation and access to UV light. Room temperature was maintained at approximately 26°C. Lizards were fed crickets dusted with vitamin supplements (RepCal), and mealworms. Water was available in small bowls, and pens were sprayed daily to provide additional moisture.

We conducted our observations in a captive setting because of the inherent difficulty in observing male–male interactions in the field. *Amphibolurus muricatus* inhabit areas of dense vegetation, which prevented us from making reliable observations in the field. As described, we made every effort to provide a natural environment. All lizards were healthy at the end of the experiment and were retained for further studies.

Procedure

We recorded the responses of captive male *A. muricatus* (resident) to a male conspecific (simulated intruder) during August 1999. We randomly selected five of the 14 lizards to act as intruders to assess variation in the responses of nine residents to different intruders. At the start of each session, one of the five intruders was randomly selected for presentation and placed in a glass tank (21 cm × 41 cm and 23 cm) positioned on a trolley outside a resident's enclosure. The back of the trolley was covered with thick black cloth to conceal the experimenter, and a piece of cardboard was positioned between the trolley and the enclosure at the start of each session. After the cardboard screen was removed, the resident's response was recorded for approximately 20 min using a video camera connected to an S-VHS video deck. We terminated the session if the resident was out of sight for the first 5 min. All sessions were conducted between 08.00 and 13.00 hours, representing the period of peak activity for our captive population (Ord 2001). We recorded a total of 48 sessions for the nine residents.

Data analysis

We began by considering the initial response of the resident to the intruder. The latency to respond, duration of the display bout (defined below), number and hold duration of push-ups, and total number of components (including repeats of the same motor pattern) were determined during frame-by-frame analysis of video footage. We determined patterns of variability by calculating coefficients of variation ($CV = SD/mean \times 100$) between and within resident males (see Robisson *et al.* 1993; Bee & Gerhardt 2001). The coefficient of variation between resident males

(CV_b) was calculated from the average response for all males, and within-resident coefficient of variation (CV_w) was determined from the variability observed within residents during filming. The ratio of between-resident and within-resident variability (CV_b/CV_w) determines the magnitude of variability observed between and within residents; a ratio greater than 1.0 indicates relatively more variability due to individual residents, whereas a ratio less than 1.0 identifies more situation-specific variability (e.g. 'quality' and behaviour of the intruder, time of day).

Body size is a reliable indicator of contest outcome in other lizard species (Tokarz 1985). It is also likely to influence the size, type and transmission distance of movement-based visual cues (Bradbury & Vehrencamp 1998). Consequently, we explored the relationship between weight and SVL, and each of the behavioural variables measured. We also looked for evidence of asymmetry in forelimb use, as has been described in toads (*Bufo bufo* and *Bufo marinus*: Bisazza *et al.* 1996). Non-parametric statistics were used to determine if there were biases in arm use. We first performed a χ^2 test of independence to determine if the arm used was independent of orientation, using a 2 × 2 contingency table. However, because lizards can contribute more than one observation per cell, we corrected the Pearson χ^2 statistic using the second-order correction of Rao and Scott (1984), to obtain an *F*-statistic. A significant result implies that either the near or far arm is preferred. We also determined whether individual lizards exhibited such biases by using Fisher's exact test. Finally, preferences for either the right or left arm for each lizard were examined using binomial tests.

We examined the serial dependencies of the display components by calculating transition probabilities. Changes in position within the enclosure were also included. We viewed footage of each session and recorded the temporal sequence of display components for each display bout by the resident. We operationally defined the start of a display bout to be the first observable movement and the finish to be after a period of at least 5 s of no movement. Immediate repetition of the same component was treated as two separate events. Transition probabilities between display components, as well as a measure of uncertainty, were calculated using the software UNCERT (Hailman & Hailman 1993). Three measures of uncertainty (*U*) were calculated based on Shannon's (see Shannon & Weaver 1949) equation for entropy (its application to the study of animal communication is fully described by Hailman *et al.* 1985). Briefly, U_0 assumes that display components are equiprobable, U_1 takes into account the actual frequency of occurrence of each component, and U_2 considers the serial correlation between adjacent components in the sequence, and is based on the matrix of transitional frequencies. A large drop between U_0 and U_1 indicates that components are

not used equally frequently. If there is little further drop to U_2, then the preceding component predicts the next one with high accuracy, and is often called semi-Markovian (see Hailman *et al.* 1985).

We analysed transition probabilities within display bouts in five ways. First, we combined all the display bouts from the 48 sessions. Second, we determined transitional probabilities for the first display bout within a given session and subsequent display bouts separately. Third, we examined whether the substrate upon which the display commenced (solid timber or foliage) influenced display patterns. We then divided the dataset according to intruder identity, and according to resident identity. For each of the these, we examined the probabilities of occurrence of each of the components as well as the probability of first-order transitions between components.

RESULTS

Initial response to intruders

Fourteen of the 48 sessions were excluded from this analysis because the display bout commenced out of camera view. Table 1 presents the average latency to respond, duration of the first tail-flick and the display bout, the average number and hold duration of push-ups, and the average number of components in the display bout. Display responses by residents occurred an average of slightly more than 4 min after the cardboard screen was removed, with most animals (32/34) remaining stationary during this period. The variance on each of these variables was then partitioned to between resident variance and mean within resident variance (see Methods). Differences between residents explained a greater proportion of the variance for both the duration of the first tail-flick and the display bout, as well as how long the push-up was held. However, there was more within-resident variation for response latency, the number of push-ups, and total number of components in the display.

There were no significant correlations between weight or SVL and response latency, duration of the first tail-flick and the full display bout, the number and hold duration of push-ups, and the total number of components. However, the correlation between CV_w for the number of push-ups performed and SVL approached significance ($r = -0.642$, d.f. = 7, $P = 0.062$), suggesting that larger lizards are less likely to vary the number of push-ups performed than smaller ones.

We observed 58 arm-wave pairs (a backward arm-wave is always immediately followed by a forward arm-wave, see next section) within the 34 initial display bouts. We categorized the lizard's orientation in the enclosure as either facing left, right, or to the front, as seen by the intruder. The frequency of use of each arm for each lizard orientation is presented in Fig. 1. We used 2×2 contingency tables to test whether the residents showed a bias toward using the near or far arm, which can be occluded by the lizard's body, as well as whether the left or right arm was favoured. Observations involving a frontally facing lizard were too infrequent for formal analysis (Siegel & Castellan 1988). We found no evidence that lizards favoured the near or far arm across the sample ($F_{1,8} = 1.21$, $P = 0.3028$) or for each lizard (probability range for
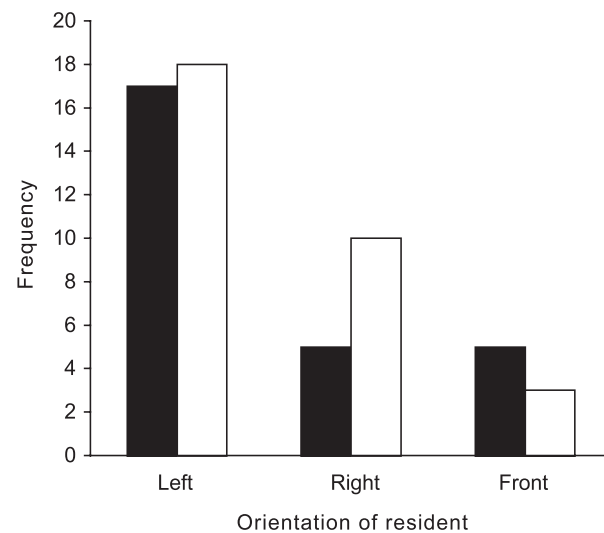

Fig. 1. Frequency of arm use by lizard orientation (as viewed by the intruder). ■), Left; □), right.

Table 1. Characteristics of the first display bout

| | Response latency (s) | Durations (s) | | No. | Push-ups | No. components |
		First tail-flick	Display bout		Hold duration (s)	
Mean	271.80	21.96	29.72	3.15	0.20	20.95
SD	110.23	30.31	30.87	1.07	0.05	1.97
CV between	40.56	138.03	103.84	33.98	25.01	9.39
CV within	80.58	86.80	73.08	38.06	12.52	12.96
CV ratio	0.50	1.59	1.42	0.89	1.84	0.72

Number of components includes repeats of the same motor pattern. CV, Coefficient of variation.

Fisher's exact test: 0.464–1.000). Binomial tests also revealed no evidence of a preference for the left or right arm (range: $P = 0.304$ to $P = 0.500$). Finally, more than half (5/9) of the resident male lizards switched arms within a display bout at least once.

Temporal structure of display bouts

We recorded a total of 402 display bouts by nine captive male *A. muricatus* in response to male conspecific intruders. The probability of occurrence of each display component for the entire dataset revealed that the push-up and body-rock components (0.29 probability of occurrence for each) were more common
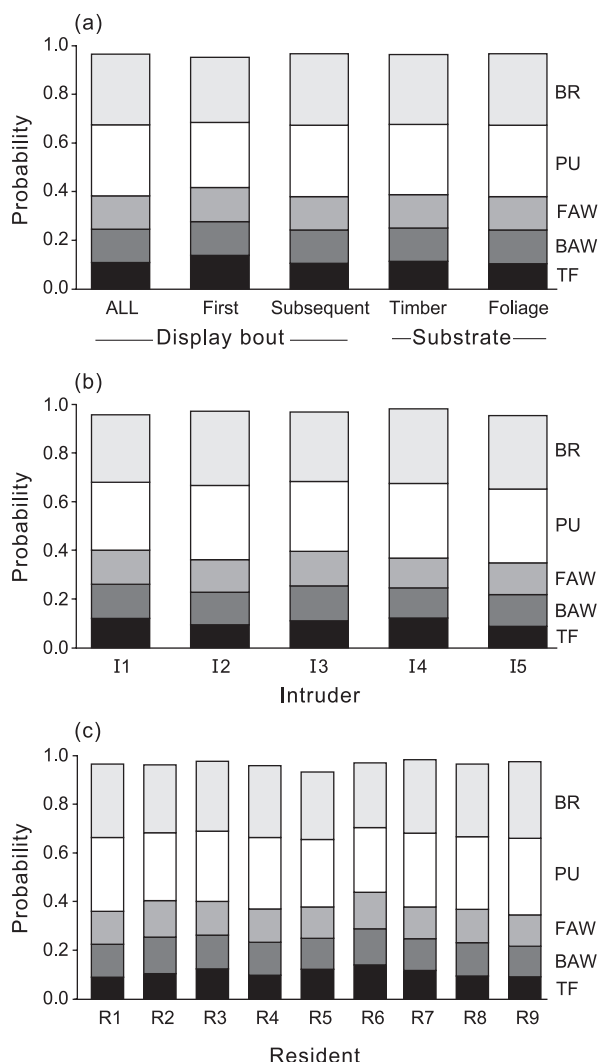
Fig. 2. The probability of occurrence of each display component: tail-flick (TF), backward arm-wave (BAW), forward arm-wave (FAW), push-up (PU), and body-rock (BR). Sequences are grouped according to (a) display bout and the substrate upon which it was performed, (b) identity of intruder, and (c) individual residents.
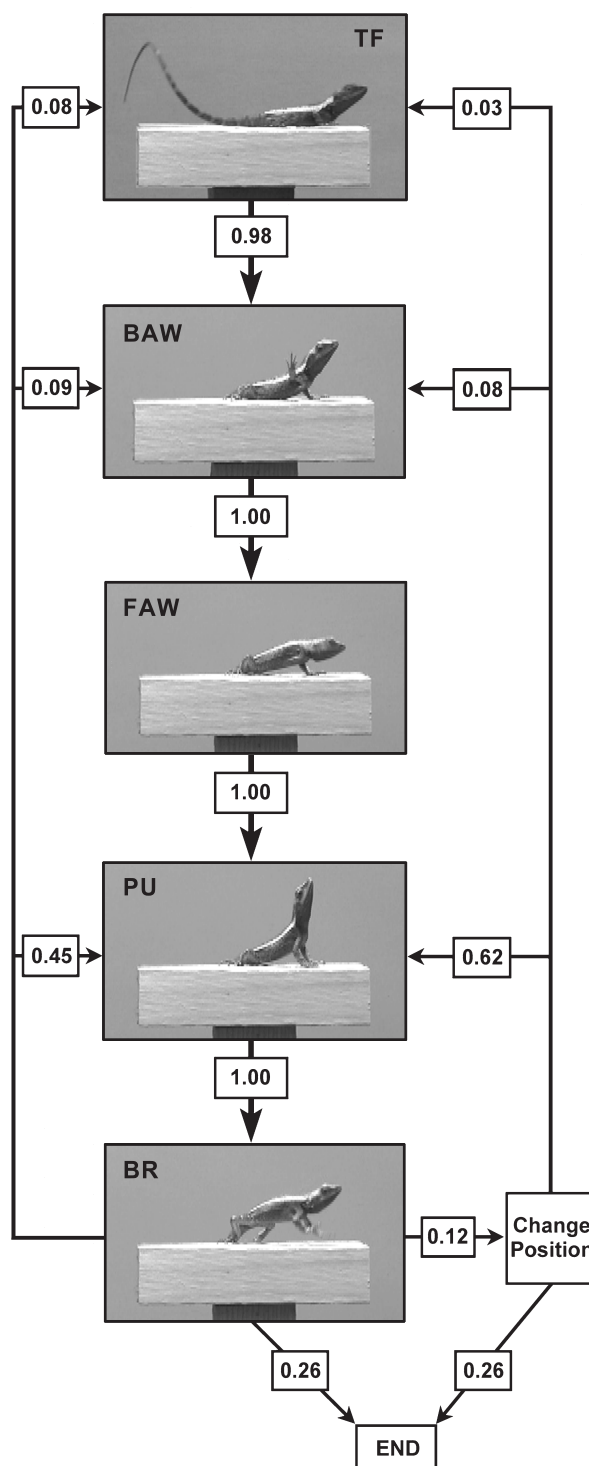

Fig. 3. Transition probabilities between components of the visual display by *A. muricatus* toward a conspecific male intruder. The display is a semi-Markovian process: a tail-flick (TF) is followed by a backward arm-wave (BAW), a forward arm-wave (FAW), a push-up (PU), and a body-rock (BR). The lizard then repeated part, or all, of the sequence, changed position or stopped. After changing position, the lizard either repeated part or all of the sequence, or stopped. (Not shown: transition from TF to PU: 0.02 probability.)

than the tail-flick, the backward arm-wave, and the forward arm-waves (0.11, 0.14 and 0.14, respectively). A shift in position within the enclosure was not common (0.04). This pattern of probabilities was consistent regardless of how we grouped display bouts (Fig. 2). The first display bout in a given session was very similar to subsequent display bouts, whereas the substrate upon which the displays were performed did not affect display component probability (Fig. 2a). Furthermore, the pattern of probabilities was consistent in response to different intruders (Fig. 2b), and by different residents (Fig. 2c).

Ninety-seven per cent of all display bouts commenced with a tail-flick. The only other component to begin a display bout was the backward arm-wave. Transition probabilities between display components for the entire dataset are presented in Fig. 3. There were no repeats of the same component, and only a body-rock or a change in position within the enclosure immediately preceded the termination of a display. The sequence: tail-flick, backward arm-wave, forward arm-waves, push-up, and body-rock, was semi-Markovian (uncertainty values: $U_0 = 2.33$, $U_1 = 0.44$, $U_2 = 0.41$); the preceding component predicted the next one with high accuracy. Almost all of the variation in the display response occurred after the body-rock. After completing a body-rock, a lizard ended the display bout (0.26 probability), changed its location within the enclosure (0.12), or repeated some or all of the components (0.62). If the lizard changed its location in the enclosure, it subsequently repeated the sequence from the push-up (0.62), or stopped (0.26).

DISCUSSION

Our analysis of the visual display of *A. muricatus* builds directly upon the original description by Carpenter *et al.* (1970). The typical response of resident males to a male conspecific intruder consisted of a movement-based visual display comprising five distinct motor patterns, or components: tail flicks, backward and forward arm-wave, a push-up and a body-rock. The proportion of each display component within any given display bout was constant (Fig. 2). This was true regardless of whether the bout was the initial or subsequent response to an intruder (Fig. 2a), irrespective of substrate (foliage or the firmer timber, Fig. 2a), intruder identity (Fig. 2b), or resident identity (Fig. 2c).

The manner in which these components were combined was also highly constrained in several distinct ways (Fig. 3). First, the initial component was almost always a tail-flick. In a companion paper, we present evidence suggesting that this component is likely designed to alert the receiver to the rest of the display (Peters & Evans 2003). Second, no component was repeated immediately. The transition from tail-flick to backward arm-wave, forward arm-wave, push-up, and body-rock was an obligatory sequence, or a semi-Markovian process. Natural phenomena can only be considered Markov processes when there is absolute certainty regarding the sequence of events (i.e. all transition probabilities are 1.0; Hailman *et al.* 1985, 1987; Hailman & Elowson 1992). The display of *A. muricatus* approximated the standard, but contained some variation in the tail-flick to backward arm-wave transition (8/514 observations). We suggest that this highly stereotyped sequence may provide a reliable cue for species identity.

Responses to intruders were also very consistent in terms of component frequency and temporal order. It is therefore likely that opponent assessment is based upon other factors. Display rate may be a good indicator of condition, particularly as movement-based displays are often energetically costly to produce (Bennett *et al.* 1981). High display rates are characteristic of dominant and aggressive lizards (Carpenter 1961; Carpenter 1963), which also tend to have larger territories and greater reproductive success (Brattstrom 1974; Dugan 1982). Recent video playback studies suggest that assessment of opponents may take place within the first few display bouts, therefore cues for assessing opponents may be available within a single display bout (Ord & Evans, in press). Our results provide some direction for investigating within-bout assessment cues. One approach would be to examine the importance of tail-flick duration. In addition to the biomechanics of negotiating a semiarboreal environment, the tail is likely to be vital for communicating with conspecifics (Gibbons 1979), which may explain why tail autotomy is not found in *A. muricatus*. An extended signal duration may also partly explain why the tail-flick is suited to an alerting function (Peters & Evans 2003). Further research is needed to establish whether lengthy tail-flicks also provide cues to receivers regarding the signaller.

The push-up component might also reveal opponent condition. Resident differences were seen in push-up hold durations, and there was also a trend for the number of push-ups performed in a given display bout to be related to body size, which is a reliable indicator of contest outcome in other lizard species (Tokarz 1985).

Another area for future investigation is the role of the arm-wave components. Some backward arm-waves were partially occluded by the lizard's body when it was orientated laterally (Fig. 1). This apparent contradiction between the predicted pattern of use based on maximization of component detection and observed foreleg choice could be explained by a side preference, as described in primates (Hook & Rogers 2000) and anuran amphibians (Bisazza *et al.* 1996). However, our data suggest that foreleg use by *A. muricatus* during

push-up displays was not biased in this way. It is possible that choice of foreleg is relatively unimportant for signal function. Whether it is partially occluded or not, it is still the least conspicuous display element, both in sweep area and velocity characteristics (Peters *et al.* 2002; Peters & Evans 2003). Such components may provide receivers with a cue for estimating the distance of the displaying male because they will only be perceptible at short distances. Many acoustic signals degrade predictively as they propagate through the environment (Morton 1982); we propose that movement-based visual displays might also have been selected to facilitate assessment of range.

Territoriality is ancestral in iguanian lizards (Martins 1994a), and the spacing patterns of *A. muricatus* suggest that they are territorial (Harlow & Taylor 2000). It is therefore likely that the displays of *A. muricatus* are an integral part of territorial defence. Such social behaviour ultimately influences spacing patterns and how animals interact with their environment. This analysis of gross display structure, combined with fine-scale analyses of display components (Peters *et al.* 2002), lays the foundation for investigations of movement-based signal design, perception and function. Furthermore, recent studies on the evolution of lizard display behaviour are biased toward North and South American iguanas (see Ord & Blumstein 2002). Therefore, complementary descriptions of the displays by other agamid lizards will create opportunities for comparative analyses and expand the study of lizard communication.

ACKNOWLEDGEMENTS

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